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Regional species richness determines local species turnover in ferns

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Abstract

The question of which factors determine the geographical change in species composition and abundance (turnover and β diversity) has typically been studied at a single scale, so that, e.g., regional-scale factors are used to explain regional turnover. But cross-scale effects are also important to understand species turnover and the spatial distribution of biodiversity in general. Here, we explored how regional richness, local forest-structure, and regional climatic factors interact to influence local species turnover. We analysed a dataset that includes the distribution of 916 fern species recorded in 1227 plots in the Bolivian Andes, forest-structure variables collected in the field, and climatic variables extracted from global databases. We used path analyses to: (i) select the best models explaining the variation in local species turnover and (ii) identify the factors that have a direct effect on species turnover and those with only indirect effects. We contrasted our results against those obtained from a null model analysis. The most important variable explaining variation in species turnover was regional species richness. We consider that this is the result of interspecific competition resulting in narrower realized ecological niches of species, although further studies are needed to confirm the mechanism. We also found that the relationship between climatic variables and local species turnover is best described by the indirect link between climatic factors and regional species richness. Our results might appear to be in conflict with previous studies finding that climatic and edaphic factors are direct predictors of local and regional variation in fern turnover. However, this is due to the different scales at which turnover was analysed. In contrast to previous studies, ours reflects the cross-scale effect of the variation in regional factors on local species turnover. Our study supports the idea that in regions with high species richness, biotic interactions strongly determine local community composition.

Highlights

- We modelled the effect of regional factors on local species turnover, an original approach in relation to previous studies.
- The variation in regional species richness explains almost all of the variation in local species turnover.
- The effect of regional environmental factors on local species turnover is indirect and mediated by regional species richness.
- The effect of local environmental factors on the variation of local species turnover is minimal when compared to the effect of regional richness.
- Because ferns are an indicator group in tropical ecosystems and our dataset spans a vast elevational gradient, our results are relevant for a better understanding of the spatial distribution of plant diversity in general.

Keywords: Andes, beta diversity, biodiversity, biotic interactions, elevational gradients, environmental drivers, ferns, Neotropics, null models, path analysis.

Introduction

Much of our understanding about spatial patterns in biodiversity is the result of the simplest type of measurement: counts of local or regional species numbers (α and γ diversity). However, besides species counts, the spatial change in species composition is also relevant to understand the distribution of diversity. Understanding the spatial change in species composition entails the study of different phenomena, among them β diversity and species turnover. We follow Tuomisto (2010b,c), who stated: “...*true beta diversity quantifies the number of compositional units (compositionally distinct virtual sampling units that have the same species diversity as the actual sampling units do on average) in the dataset*”. The study of true beta diversity requires species abundance data, which are missing in our otherwise extensive dataset. Therefore, we focused on the *effective species turnover*, a component of β diversity that “*quantifies the number of species that change among all compositional units in the dataset*” (Tuomisto 2010c) and that is quantified using presence-absence data.

Turnover reflects the variation in spatial arrangements of species ranges and communities. Thus, areas with high levels of turnover typically have small, patchily distributed species populations at local scales, and at larger scales concentrations of endemic and range-restricted species, rendering them important targets for conservation. Mountains commonly have higher levels of species turnover than lowland areas at both regional (Mourelle and Ezcurra 1997, Kessler 2000a, Kluge et al. 2008) and continental (McKnight et al. 2007) scales. This is linked to the great variety of habitat conditions as well as the topographic complexity of mountains, which render them vital for the generation and maintenance of biodiversity (Fjelds  et al. 2012, Wang et al. 2012, Hoorn et al. 2013, Antonelli 2015, Hughes and Atchison 2015), especially under climate change conditions (Sandel et al. 2011). Mountain ecosystems are therefore key priorities for conservation using strategies that take into consideration patterns of species turnover (Socolar et al. 2016).

Species turnover and β diversity are determined by numerous factors, including the biology of the studied organism, e.g., their dispersal ability (Linares-Palomino and Kessler 2009), interspecific interactions (Callaway et al. 2002, Wardle 2006), and especially environmental gradients, e.g., temperate vs tropical areas (McKnight et al. 2007, Qian and Ricklefs 2007), and more specifically temperature (Fitzpatrick et al. 2013), humidity (Richard et al. 2000, Karst et al. 2005, Jankowski et al. 2009), soils (Tuomisto et al. 2002, 2003a,b,c, Jones et al. 2006), productivity (Harrison et al. 2006), and species richness (Jost 2007, 2010, Tuomisto 2010a, De C ceres et al. 2012, Ulrich et al. 2017). The influence of geographical distance can be the result of environmental gradients (Nekola and White 1999) or of variation in the dispersal capacity of the species (Hubbell 2001). In addition, estimates of species turnover depend on sampling design (size, number and arrangement of samples) (Kraft et al. 2011, Qian et al. 2012, Tuomisto and Ruokolainen 2012).

Previous evidence suggests that species turnover also varies along gradients of species richness (McKnight et al. 2007, Qian and Ricklefs 2007). Changes in species richness can influence species turnover in three ways. First, if sampling units are so small that they only include a small percentage of the regional species pool, then in species-rich regions turnover between sampling units will be high because it is less likely that two samples will include the same species. The opposite occurs if the samples are so large that each of them contains most species from the regional pool (Jost 2007, Tuomisto 2010b, Karger et al. 2015). Second, higher regional species richness can lead to more interspecific competition, resulting in narrower realized ecological niches of species (Karger et al. 2015) and hence higher turnover. Finally, if sampling units have a significant variation in species richness independently from their size, we expect turnover to vary accordingly, simply because communities of different richness by default cannot be identical. However, few studies (e.g., Lenoir et al. 2011) have explored the relative importance of species richness in relation to other ecological gradients.

The study of turnover in plants has established that different environmental factors influence their turnover according to the ecological requirements of the species (Chapin et al. 1987, Svenning 2000, Silvertown 2004, Jones et al. 2006, 2011, 2013, Kr mer et al. 2007). Nevertheless, the strength of this relationship may vary along an environmental gradient (Huston 1999, Callaway et al. 2002, Duque et al. 2002, Tuomisto et al. 2003a, Zuquim et al. 2012), and the question is which factors dominate under which conditions? Studies in tropical areas have found that the importance of different factors differs depending on the amount of environmental variation. For instance in western Amazonia, where there is high topographical structure and therefore high environmental heterogeneity (Hoorn et al. 2010), species turnover is correlated with factors like inundation regime and soils (Tuomisto et al. 2003a, Kristiansen et al. 2012, Draper et al. 2017), and similar results were found in rainforests of Costa Rica (Jones et al. 2006) and Panama (Jones et al. 2013). In mountain regions, where large environmental heterogeneity occurs over relatively small distances, besides soil heterogeneity other environmental factors like moisture and temperature play an important role in explaining species turnover (Kessler 2000a, Kluge et al. 2008, Jones et al. 2011, but see Jones et al. 2014).

The influence of different factors can also change with spatial scale and the environmental factors associated with it. Therefore, species turnover and beta diversity have been studied at different extents and grain sizes (e.g., Condit et al. 2002, Tuomisto et al. 2003a,b, Jones et al. 2006, 2013, Harrison et al. 2006, McKnight et al. 2007, Novotny et al. 2007, Qian and Ricklefs 2007, Soininen et al. 2007, Myers et al. 2013). Within these studies, the drivers of turnover are typically studied at a single scale, so that, e.g., regional-scale factors are used to explain regional turnover. But cross-scale effects are potentially also important to understand the factors determining species

turnover. For example, turnover at a local scale varies over regional scales with elevation (McKnight et al. 2007, Melo et al. 2009), temperature, and the size of the regional species pool (Mourelle and Ezcurra 1997, Tello et al. 2015). However, cross-scale factors have received limited research attention so far.

In the present study, we assessed the effect of species richness on local species turnover and its relative importance in relation to environmental factors at local and regional scales. We did so by analysing a data set of 1227 plots established in 62 localities across the Bolivian Andes that contains 916 fern species (77.3% of the Bolivian fern flora; Kessler and Smith 2017) and covers the main forest types and climatic variation of the country (Fig. 1). Ferns are a suitable group of plants for this kind of study because they occur with fairly high species numbers across a wide range of forest habitats (Kessler 2000a,b, Kessler et al. 2011, Salazar et al. 2015), have a reasonably well-known taxonomy (PPG I 2016, Kessler and Smith 2017), and because their spore dispersal reduces the effects of dispersal limitation (Barrington 1993, Linares-Palomino and Kessler 2009).

We explored two main questions: Do regional climate, regional and local forest structure, and species richness relate to local species turnover directly or through the interaction between them? And what is the relative importance of regional climate, regional and local forest structure, and regional species richness in explaining the variation in local species turnover? We used path analysis to identify the variables and interactions determining fern species turnover. We included three groups of explanatory factors. The first one being the mean number of species per plot in each site (hereafter regional species richness); the second group included variables related to forest structure (bryophyte, canopy, and plant cover) and also measured at the plot level; finally, the third group included climatic variables (elevation, precipitation,

temperature, soil cation exchange capacity (CEC) and soil pH) extracted for each site at the regional scale from the global models CHELSA and SoilGrids. Our hypotheses were that: (i) local species turnover is best described by a combination of local and regional environmental factors that interact between them; ii) regional species richness strongly determines local species turnover by controlling the amount of species to be 'accommodated' in each plot; and finally, iii) the influence of local environmental factors is higher when they are linked to a regional factor that is limiting.

Methods

We used a large dataset of 1227 plots sampled in 1995–1997 and fully described in Kessler (2000a,b) and Salazar et al. (2015), distributed across 62 sites in Bolivia (Fig. 1a). The plots contain a total of 916 fern species (77.3% of the Bolivian fern flora; Kessler and Smith 2017). Sites ranged from 200 m to 3740 m in elevation, 550 mm to 3500 mm in mean annual precipitation, and 8°C to 25°C in mean annual temperature, thus covering most climatic conditions where forests occur in Bolivia (Fig. 1b). Sites covered different elevational ranges and forests with varied habitat conditions including rock faces, ravines, primary and secondary forests. We did not sample non-forest biomes (savannahs or alpine vegetation) because ferns are very poorly represented in them. We attempted to survey 20 plots per site. However, the number of plots at each site ranged from 9 to 44 plots (mean = 21 plots). The main reason for the variation in the number of plots was the lack of habitat in some areas and the ease of access and inventory in others. Importantly, the number of plots per site did not have any relationship to the number of species recorded (Fig. S1) and therefore did not bias our results.

Each plot was 400 m², a size considered as the minimum area required for representative sampling

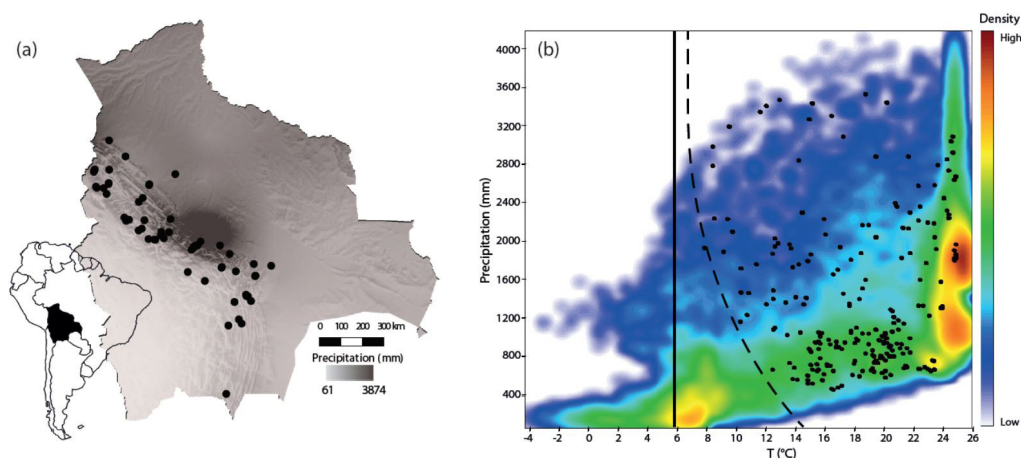


Figure 1. Study area. Precipitation map of Bolivia showing our 62 study sites (a). Distribution of plots in a density diagram representing the climatic conditions (mean annual temperature vs. mean annual precipitation) of Bolivia (b). The solid line shows the approximate climatic limit of the tree line following Körner and Paulsen (2004), and the dashed line shows the current limit of the tree line mainly determined by human disturbance (Fjeldsø et al. 1996). Note that the study sites cover most of the available climatic space within the range of extant forest biomes.

of ferns and small enough to sample a homogeneous environment (Kessler and Bach 1999). The environmental variables recorded in each plot and used for the present study included: elevation, recorded with a handheld Eschenbach altimeter and using 1:250,000 topographic maps to correct for inaccuracies; epiphytic bryophyte cover, visually estimated as the percentage of canopy branches covered by bryophytes, and used as a proxy for air humidity (Karger et al. 2012); canopy cover recorded as the percentage of canopy covered by trees; and ground plant cover, recorded as the percentage of ground covered by plants. We also extracted the regional values of mean annual precipitation and mean annual temperature from the BIOCLIM V1.1 layers of the global CHELSA model at 1 km² resolution (Karger et al. 2017), and the values of cation exchange capacity (CEC) and pH from the global 'SoilGrids' database at 1 km² resolution and 1 m depth (Hengl et al. 2017). All variable units are summarised in Table 1. In each plot, all fern species (terrestrial and epiphytic) were identified and counted, treating terrestrial and epiphytic plants separately. Voucher specimens were collected and deposited in the herbaria in La Paz (LPB), Göttingen (GOET), and Berkeley (UC). Individuals were classified to the species level, and nomenclature was unified according to PPG I (2016) and Kessler and Smith (2017) based on two decades of taxonomic work on Bolivian ferns by M. Kessler and A.R. Smith (UC Berkeley). Unidentified individuals (<4%), usually sterile juvenile plants, were excluded from analyses. In total, our dataset contained information on the distribution of 23029 occurrences (plot-records) of 916 species.

Data analysis

Turnover estimates

β diversity can be expressed as a rate or as a difference. In the former case, β diversity is considered as the fraction of the total (γ) richness distributed among local sites (α). In the latter case, β diversity is treated as the dissimilarity in species composition between sample units (Whittaker 1972, Anderson et al. 2011, Tuomisto 2010a). Here we follow the terminology of Tuomisto (2010a,b,c) whereby assessing purely the change in species composition refers to species turnover and not β diversity in the strict sense, which also considers changes in species abundances and their relation to gamma diversity. As such, here we only consider one of the components of β diversity, that of compositional differentiation.

Specifically, in this study we defined local turnover as the dissimilarity in species composition between plots belonging to the same site. We obtained dissimilarity values using presence-absence matrices for each site (rows = species, columns = plots) and independently for terrestrial (62 sites) and epiphytic (58 sites) ferns. We used the function 'vegdist' from the R package *vegan* (Oksanen et al. 2018) to obtain the dissimilarity in species composition between all plots within each site using the 'binary euclidean' index with the formula:

$$d[jk] = \sqrt{A + B - 2 * J}$$

where j and k correspond to each pair of plots, A and B to the number of species in j and k , respectively, and J equals the number of species shared between both plots.

This index is appropriate for presence-absence data and it quantifies the relative number of species that change among plots (Tuomisto 2010c). Using this index, we calculated the dissimilarity of plot A vs all other plots in the same site and then used the mean of these dissimilarities as our measure of within-site turnover. The mean pairwise distance is a robust estimate of species turnover regardless of the number of samples (Marion et al. 2017). For further statistical analyses, we used this mean dissimilarity value of each site, and hereafter refer to it as local turnover. Thus, we obtained 62 measurements of local turnover for terrestrial ferns and 58 measurements for epiphytic ferns. Local turnover varies from low values when many species are shared between plots and larger values when few species are shared. Because plots were assumed to have been fully sampled (i.e., no missing species), we did not correct turnover values for sampling incompleteness.

Path Analysis

For this analysis we used the climatic variables, the mean values for each forest-structure variable and mean species richness as a surrogate of regional variation between sites, and the coefficient of variation of each forest-structure variable and species richness as a surrogate of local (plot to plot) variation. We did not include elevation in the path analyses due to its high correlation (>60%) with annual temperature.

We defined a first set of models to address our main questions: Do regional climate, regional and local forest structure, and species richness relate to local species turnover directly or through the interaction between them? And what is the relative importance of regional climate, regional and local forest structure, and regional species richness in explaining the variation in local species turnover? Hereafter we refer to this set of models as set 1 or regional + local models. This set consists of three models (Fig. 2, left panel). In the first one, each group of variables was allowed to interact directly with species turnover ('direct'). The second one only allows the direct interaction of local structure and richness with turnover, whereas regional climate must first interact with regional structure and richness and these with local variables ('indirect'). Finally, the third model allows both regional and local variables to interact directly with species turnover, whereas regional climate can only act through a link with regional structure and richness ('direct + indirect'). These path analyses were performed using the R packages *lavaan* (Rosseel 2012) and *semPlot* (Epskamp 2019).

The results of the first set of models showed that regional factors were more important in explaining local species turnover (see Results). Therefore, we defined a second set of models (Fig. 2, right panel, hereafter referred to as set 2 or regional models) to address the following specific queries: is variation in local species turnover better explained by: (i) a model

Table 1. Variables selected for the path analyses. Variables were recorded in each plot (i–v) and extracted for each plot from SoilGrids (vi–vii) and CHELSA-BIOCLIM V1.1 (viii–ix).

Variable name	Biotic variables		Forest structure variables			Regional climatic variables			
	i	ii	iii	iv	v	vi	vii	viii	ix
Local species richness	Local species richness	Regional species richness	Bryophyte cover	Plant cover	Canopy cover	Soil pH	Cation exchange capacity	Mean annual temperature	Mean annual precipitation
Description or units	Coefficient of variation of the number of species per plot	Mean number of species per plot	Estimated % of branches covered by bryophytes	Estimated % of ground covered with plants	Estimated % of canopy covered with plants	-log([+H])	mmol(c)/kg	(°C)	(mm/year)

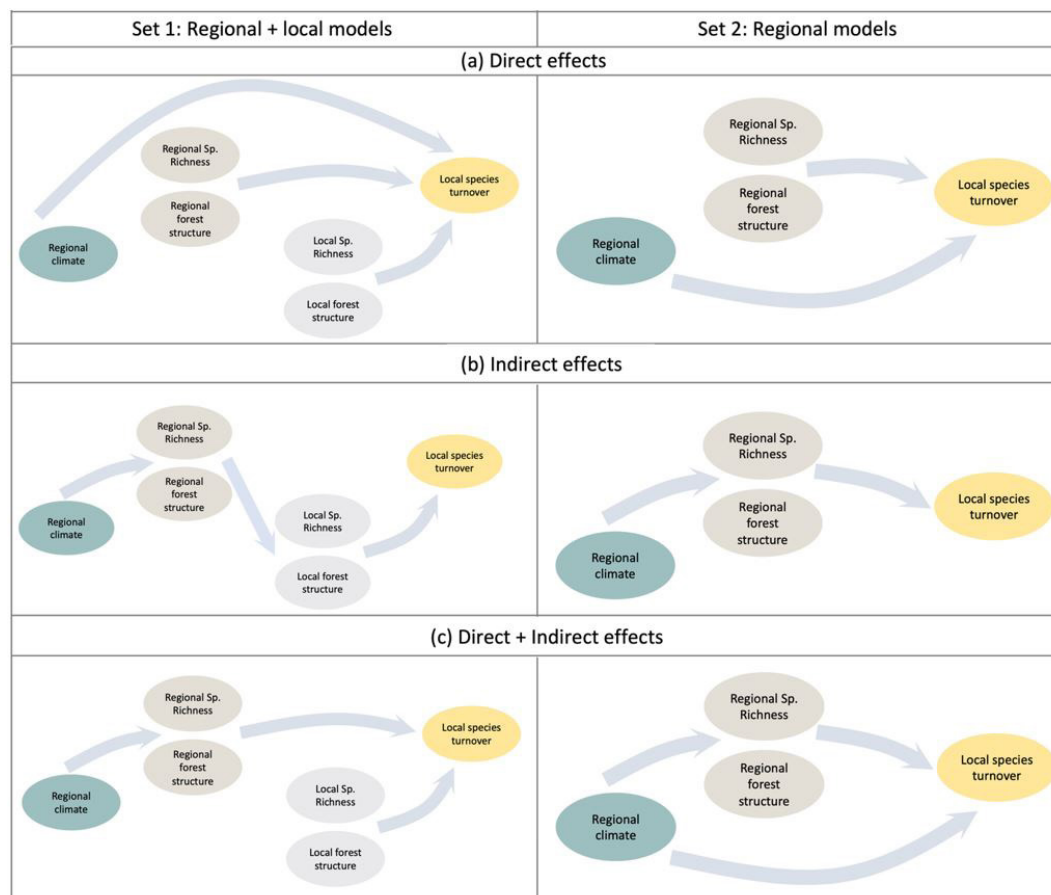


Figure 2. Models tested using path analyses. Set 1 (left) includes both regional and local predictors; this set showed that mostly regional factors were important predictors, thus Set 2 (right) tests the interactions and importance of only regional predictors.

where climatic variables, regional forest-structure, and regional species richness interact directly with it ('direct'), (ii) a model where climate is first linked to regional variables and only the latter are linked to species turnover ('indirect'), or (iii) a model where climatic variables and species turnover are allowed to interact directly and also through the interaction with regional variables ('direct + indirect'). We tested the goodness of fit of the resulting models using a χ^2 (Chi-square) test and separately for each set of models. The extraction of climatic and soil variables and all statistical analyses were carried out in the programming environment R (version 3.5.3, R Core Team, 2019).

Null models

To assess if regional richness is a consistent predictor of the variation in local species turnover we carried out a null model analysis. First, to test the effect of local variation in species richness, we randomised all presence-absence matrices using the algorithm 'Sim2' from the R package *EcoSimR* (Gotelli and Ellison 2013). Sim2 is recommended for plot datasets and was suitable for our test because it preserves differences in the frequency of species across sites, i.e., the row

sums, but assumes that all plots are equiprobable (Gotelli 2000). Using these null matrices, we again calculated local species turnover and performed the path analysis, as described above. We expected that regional richness would be the main predictor of the random local turnover because by making all plots equiprobable, we randomised the effect of local variation, thus the variation in local species turnover should still be determined by the differences in the number of species in each site.

Second, we randomised the values of regional richness in the data frame used to calculate the path analysis and ran the analysis again. Here, we expected that the relationship between local species turnover and regional richness would be disrupted and therefore other factors would predict the variation of the former.

Finally, to discard the possibility that our results were an artefact of the large habitat variation covered by our sampling, we re-ran all our analyses using a subset of data that contained only plots located in zonal forests (758 plots), i.e., in mature forests without the presence of rock faces, ridges, lakeshores, ravines, swamps, grasslands, or plantations. These results did not differ significantly from those obtained using the complete dataset and therefore are not shown.

Results

The first set of models showed that the 'direct model', which allowed the direct interaction of all variables with species turnover, explained a large proportion of variation in species turnover, but this model had the worst fit to the data. The 'indirect model', allowing the interaction first from regional-climate then to regional factors and finally to local factors, explained a small amount of the variation in local species turnover for terrestrial and epiphytes and had the second-best fit to the data. Finally, the 'direct + indirect' model, where regional climatic factors interacted only with regional forest-structure variables and without a link between regional and local variables, explained a large proportion of the variation in species turnover for both terrestrial and epiphytes and had the best fit to the data. In these three models, regional species richness was the most important factor explaining the largest percentage of variation (Table 2, Fig. 3).

The second set of models confirmed that for both epiphytes and terrestrial ferns, regional richness is the factor controlling almost the totality of the variation in species turnover. Certainly, the best fitted models were those where climatic variables interacted both directly with species turnover and also through the interaction with regional species richness (Table 2). In consequence, local turnover was highly dependent on regional species richness, and also in a small but significant proportion to regional climatic factors (Fig 3.) Figure 3 shows the path diagrams for the best fitted models and statistics for the rest of models can be found in Tables S1 and S2.

According to the best fitted models (i.e., Set 2 'direct + indirect'), after regional species richness, the factors that were significantly related to fern turnover differed for terrestrial and epiphytic ferns. These factors

explained a very small percentage of variation in local turnover and were regional bryophyte cover and CEC for terrestrial ferns and soil pH for epiphytes (Fig. 3).

Regarding environmental covariates in models for terrestrial ferns, CEC and pH were important covariates of terrestrial regional species richness, and annual temperature and annual precipitation were important covariates of bryophyte cover. Similarly, the models for epiphyte ferns showed CEC and pH were important covariates of epiphytic regional species richness (see Table S2 'Observed results' for all factor loadings).

The null models corroborated that regional richness is the main predictor of the variation in local species turnover and that this relationship is not merely the result of a numerical autocorrelation between species turnover and species richness. In the first test, where local variation in species richness was randomised, regional species richness was maintained as the most important predictor of local species turnover. In the second test, where regional species richness was randomised across all sites, other factors different to regional richness were the best predictors of local species turnover (see Table S2 'Null models' for all factor loadings).

The specific relationship between local species turnover (within site) and regional species turnover is shown in Fig. 4a,c. In addition, panels b and d show that the variation in local species richness could not bias our results because there is not a positive response of local turnover to an increasing local richness.

Discussion

In agreement with our hypothesis (ii), we found that by far the strongest predictor of local species turnover was the variation in regional species richness. In response to our questions on the relative importance

Table 2. Summary of models fit and X^2 tests for models explaining species turnover of ferns in local plots across 62 (terrestrial ferns) and 58 (epiphytic ferns) study sites along an elevational gradient in the Bolivian Andes. See figures 2 and 3 for details about models set (1 or 2) and type ((a), (b) or (c)). Tucker-Lewis Index (TLI), Root Mean Square Error of Approximation (RMSEA). **p-value < 0.001, *** p-value < 0.0001

Habit	Model	TLI	RMSEA (confidence interval)	X^2 test
SET 1				
Terrestrials	(a) Direct	1	0	
	(b) Indirect	0.325	0.246 (0.216 – 0.277) ***	88.365 ***
	(c) Direct + indirect	0.739	0.263 (0.223 – 0.304) ***	158.223 ***
Epiphytes	(a) Direct	1	0	
	(b) Indirect	0.214	0.274 (0.242 – 0.306) ***	111.64 ***
	(c) Direct + indirect	0.716	0.290 (0.248 – 0.334) ***	162.22 ***
SET 2				
Terrestrials	(a) Direct	1	0	
	(b) Indirect	0.615	0.233 (0.175 – 0.295) ***	19.041 **
	(c) Direct + indirect	0.512	0.263 (0.188 – 0.343) ***	42.196 ***
Epiphytes	(a) Direct	1	0	
	(b) Indirect	0.678	0.214 (0.156 – 0.275) ***	2.010
	(c) Direct + indirect	0.551	0.253 (0.188 – 0.322) ***	55.787 ***

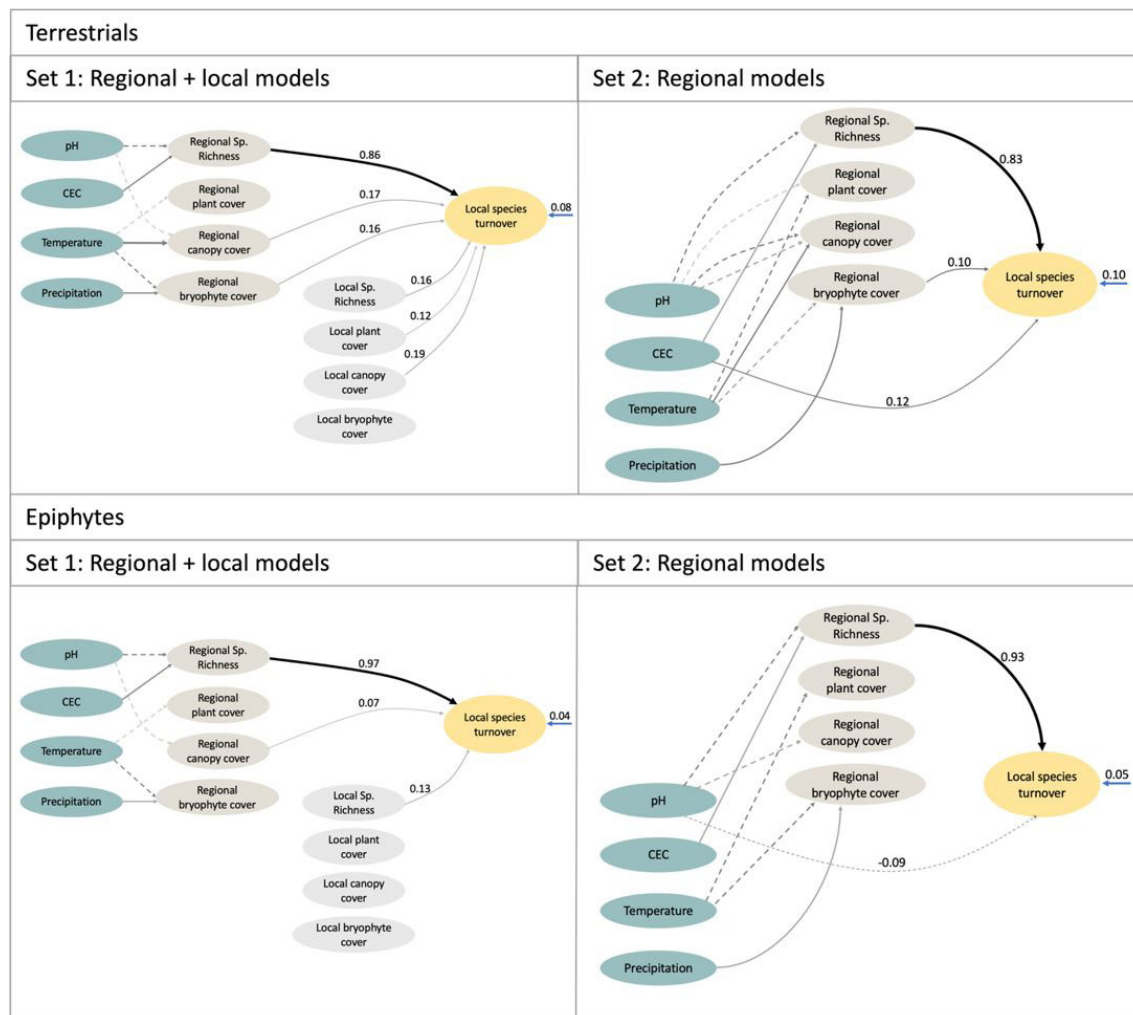


Figure 3. Best fitted models for the factors determining local species turnover along an elevational gradient in Bolivia. For both terrestrial and epiphytic ferns and in both sets of models, the best goodness of fit was found for ‘direct + indirect models’, which correspond to models C in Fig. 2. Only significant relationships were included as lines, line discontinuity and boldness represent the strength of the relationship. (See Table 2 for summary statistics and Tables S1 and S2 for statistics of the rejected models and individual factor loadings for all models including the non-significant coefficients excluded from this figure).

and interaction between local and regional factors, we found that regional factors were relatively more important than local factors in explaining local species turnover. However, we did not find support for our hypotheses (i) and (iii) because the explanatory power of local factors was minimal compared to regional species richness.

Overall, we found that sites with high species richness had high turnover between study plots, whereas sites with low richness had low turnover. This pattern, which has also been found in previous studies on plant species turnover (McKnight et al. 2007, Qian and Ricklefs, 2007), could be the result of three different and mutually non-exclusive mechanisms.

First, sampling units might be so small that they can only contain a limited number of fern individuals, thereby limiting the potential number of species in each plot (Jost 2007, Tuomisto 2010b, Karger et al.

2015). We consider this to be unlikely in our case because ferns are typically quite small and we have recorded up to several thousand individual plants in single plots of 400 m², which is much higher than the number of species recorded (about 10 on average per plot, with a maximum of 82 species). This is further supported by the fact that in our data the number of species per site does not increase with its number of plots (Fig. S1). However, to truly test this mechanism, we would need to sample plots of different sizes to assess the effect of plot size and number of individuals on species turnover.

Second, the effect of differences in species richness on species turnover may be a sampling effect (Baselga 2007, Tuomisto 2018): two samples (plots) with very different species richness cannot have high compositional similarity, even if the species-poor sample is a perfect subsample of the species-rich one. Thus, two samples can only have high similarity if they have

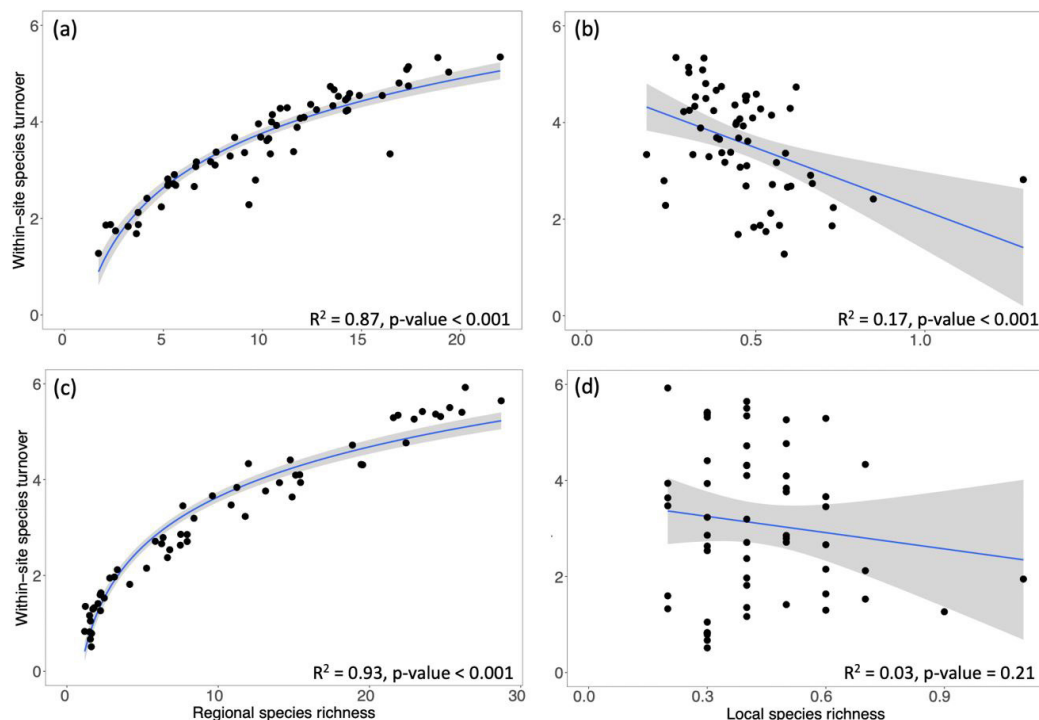


Figure 4. Local (within site) species turnover in relation to regional and local species richness. The relationship is shown for terrestrial ferns (upper panels) in 62 sites and for epiphytic ferns (bottom panels) in 58 sites distributed across the Bolivian Andes. Here, regional species richness is a surrogate that corresponds to the mean number of species per plot in each site, whereas local species richness corresponds to the coefficient of variation in the number of species per plot in each site. Shaded areas indicate the 0.95 confidence intervals. We produced three types of models: linear, logarithmic, and polynomial. We then selected and plotted the best fit using the Akaike Information Criterion (AIC) (see Table S3 for model formulas, statistics and AIC values). Plots were produced with the R package *ggplot2* (Wickham 2016).

similar species richness, although of course they can also be dissimilar. Again, we consider that this effect is unlikely in our case because it would have been captured by the variability of species richness between plots at a site and this factor was not recovered as important in our path models (Fig. 3). Moreover, the relationship was negative (Fig. 4b,d), so that sites with large variation in richness between plots had low turnover, and vice versa, which is opposite to what this mechanism predicts. Rather, it was the regional variation in species richness, i.e., differences between sites rather than between plots at a site, that was the important predictor of turnover.

Third, higher regional species richness might lead to more interspecific competition, resulting in narrower realized ecological niches of species and hence higher turnover, or alternatively, narrower niches might lead to less competition, greater niche packing and greater richness. While our data does not allow us to test these possibilities directly, we consider them as likely causes since Karger et al. (2015), using a similar sampling approach, found that the realized niches of fern species were narrower on large tropical islands with a high regional species richness than on small islands with a limited species number. In addition, a study in Ecuador found that plots with high numbers of fern individuals tend to have lower species numbers than

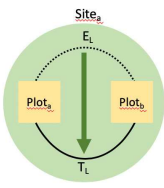
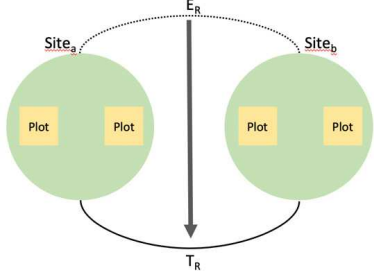
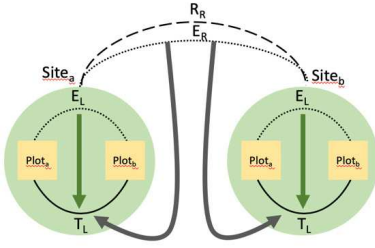
plots with fewer individuals because in the former a few species excluded weaker competitors (Kessler et al. 2014). Both of these studies point to the importance of interspecific competition in species-rich tropical fern assemblages. Thus, although additional studies would be needed to specifically test the different potential mechanisms, we consider that the high spatial turnover in species-rich fern assemblages is largely the result of interspecific competition and resulting narrower realized niches of the individual species.

In addition to regional species, we also found a significant - even if indirect - influence of climatic factors in our models, which is in line with previous studies showing that patterns of species turnover in mountains are strongly influenced by climatic and habitat conditions (Mourelle and Ezcurra 1997, Kessler 2000a, Kessler et al. 2001, McKnight et al. 2007, Jones et al. 2011, Tello et al. 2015). This is the direct result of microhabitat changes in factors like temperature and light (Cortés and Wheeler, 2018) that result from the high spatial variability of factors such as elevation, aspect, inclination, and landscape arrangement in mountain systems (Fjeldsø et al. 2012, Wang et al. 2012, Hoorn et al. 2013, Antonelli 2015, Hughes and Atchison 2015). However important all these effects are, we found that the relationship between the climatic variables and species turnover is better

described by the indirect link between climatic factors and regional species richness. Fern species richness is strongly influenced by climatic variables, being high in cool and humid regions, low in regions with very low or high temperatures, or low precipitation (Kreft et al. 2010, Kessler et al. 2011, Weigand et al. 2020).

The strong influence of regional species richness on local species turnover in Andean fern assemblages might at first glance appear to be in conflict with previous studies finding that climatic and edaphic factors are direct predictors of local and regional variation in fern turnover, as summarized in Box 1. However, this

Box 1. Turnover and beta diversity studies of ferns and their spatial scales. Previous studies used local predictors to study differences in fern species composition and diversity at local sales (a) or regional predictors to explain differences at regional scales (b). In our study, we attempted to use both local and regional predictors to understand the differences in local fern species turnover (c). The best predictors of species turnover or beta diversity in each study are given in *italics*. *Studies at broader than regional scales.

(a) Local species turnover or beta diversity vs Local predictors	(b) Regional species turnover or beta diversity vs Regional predictors	(c) Local species turnover vs Regional predictors
		
Diagrams legend: squares = plots within sites, circles = sites, E_L = variation in local environment, E_R = variation in regional environment, R_R = Variation in regional richness, T_L = local species turnover, T_R = regional species turnover, green arrows = effect of local factors, grey arrows = effect of regional factors.		
da Costa et al. 2018: <i>Local temperature, luminosity, soil moisture.</i>	de Gasper et al. 2013: <i>Air humidity, geographic distance.</i>	This study: <i>Regional richness</i>
da Costa et al. 2019: <i>soil base cation content, rock cover.</i>	Harrison et al. 1992: <i>Day length, temperature, rainfall.</i>	
Jones et al. 2006: <i>Soil nutrient content, drainage, canopy openness.</i>	Kessler 2000a: <i>Rainfall, soil texture and nutrient content, vegetation structure.</i>	
Jones et al. 2008: <i>Soil nutrients content, slope, topography.</i>	Kluge et al. 2008: <i>Humidity, forest structure.</i>	
Jones et al. 2011: <i>Microclimatic conditions associated to temperature, humidity, slope and aspect, soil conditions.</i>	*Qian and Ricklefs 2007: <i>geographic distance at the continental scale, environmental distance at the regional scale.</i>	
Jones et al. 2013: <i>Dry season length, soil nutrients (P, pH, Ca).</i>	*Qian 2009: <i>Dispersal ability (measured as latitude).</i>	
Jones et al. 2014: <i>Soil nutrients (Ca, Mn), elevation.</i>	Tuomisto et al. 2003a: <i>Soil type and content of exchangeable bases (Ca, K, Mg, and Na).</i>	
Nettesheim et al. 2014: <i>Local climate associated to topography.</i>	Tuomisto 2006: <i>Soil inundation, soil base cation content, soil texture.</i>	
Schietti et al. 2014: <i>vertical distance from water table.</i>	* Tuomisto et al. 2019: <i>Soil base cation concentration, climate.</i>	
Tuomisto et al. 2003b: <i>Topography and general soil characteristics.</i>	Watkins et al. 2006: <i>Elevation.</i>	
Tuomisto et al. 2003c: <i>Soil characteristics (Ca, K, Mg, clay, sand, organic material).</i>	Zuquim et al. 2012: <i>Soil base cation and clay content.</i>	

is due to the different scales at which turnover was analysed. Our results reflect the cross-scale effect of the variation in regional factors (between sites) on local species turnover (between plots). In contrast, e.g., Tuomisto et al. (2003a) studied regional turnover between sites in relation to environmental differences between sites, whereas other studies like Jones et al. (2006, 2011, 2014) looked at local variation in community composition in relation to local factors. It would thus appear that at a given scale (either regional or local), turnover in species assemblages is closely linked to environmental factors. However, our models also allowed for a direct effect of all local variation in forest-structure parameters, including local species richness on turnover, but their effect was minor and overridden by the regional effect of species richness.

Finally, the variation that was not explained either by our main or residual models might reflect the lack of data on important environmental variables (Harrison et al. 2006, Zuquim et al. 2012), biotic interactions such as competition or facilitation between ferns as well as with other plants or animals (Callaway et al. 2002, Wardle 2006), and stochastic variation (De Cáceres et al. 2012, Karst et al. 2005). For example, studies in Ecuador have shown that around half the fern species in plots of 400 m² are only represented by a few sterile individuals, most likely as the result of sporadic colonization events that are unlikely to result in persistent populations in a given plot (Kessler et al. 2014) but that can greatly influence the perception of diversity patterns (Kessler et al. 2011). In our study, we were unable to decide which species in a plot would belong to the “core” flora and which ones were only transient “visitors”, so we were unable to assess the potential influence of the latter.

Conclusions

In combination with a series of other studies, our results provide evidence that spatial turnover of tropical plant assemblages is driven by different factors at different scales. On the one hand, there is the self-evident importance of environmental heterogeneity in determining patterns of biodiversity and community composition, especially in mountain settings (Fjeldsø et al. 2012, Hoorn et al. 2013, Wang et al. 2012, Hughes and Atchison, 2015, Sandel et al. 2011). On the other hand, we found that there is also an important effect of regional variation in species richness on local species turnover, presumably driven by interspecific competition. Ecologists have long debated the relative importance of abiotic and biotic factors in determining the richness of tropical plant communities and their spatial variation, and our study provides support for the idea that in species rich communities the importance of biotic interactions increases. This is because on the one hand species-rich communities typically have environmental conditions that are not overly stressful for the organisms under consideration and on the other hand because high species richness increases the opportunities for biotic interactions.

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Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Figure S1. Regression model for the number of plots and the total number of species recorded in each of 62 study sites along an elevational gradient in the Andean mountains.

Table S1. General estimates and significance of all models tested to explain species turnover of ferns in local plots across 62 (terrestrial ferns) and 58 (epiphytic ferns) study sites along an elevational gradient in the Andean mountains.

Table S2. Summary of statistics and individual factor loadings for all models tested using the observed and random (null) data.

Table S3. Evaluation of local turnover vs regional richness models.

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